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*Original Citation:*

*Availability:*

This version is available <http://hdl.handle.net/2318/136203> since 2016-07-05T22:16:22Z

*Published version:*

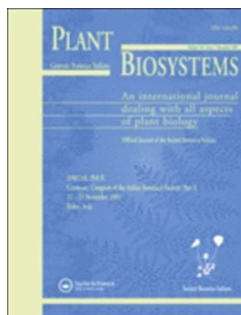
DOI:10.1080/11263504.2013.819821

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(Article begins on next page)



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Journal:	<i>Plant Biosystems</i>
Manuscript ID:	TPLB-2013-0057.R1
Manuscript Type:	Original Article
Date Submitted by the Author:	n/a
Complete List of Authors:	Vacchiano, Giorgio; Università di Torino, Department of Agricultural, Forest, and Food Sciences Lonati, Michele; Università di Torino, Department of Agricultural, Forest, and Food Sciences Berretti, Roberta; Università di Torino, Department of Agricultural, Forest, and Food Sciences Motta, Renzo; Università di Torino, Department of Agricultural, Forest, and Food Sciences
Keywords:	Ellenberg indicator values, Plant diversity, Resilience, Restoration, Wildfire

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Running title: Post-fire regeneration of Scots pine

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# Drivers of *Pinus sylvestris* L. regeneration following small, high-severity fire in a dry, inner-alpine valley

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## Abstract

In dry, inner-alpine valleys, regeneration of Scots pine after large, high-severity fires is limited by seed dispersal distance. When dispersal limitations are relaxed (small fires), colonization dynamics of Scots pine remain unclear. Our aims were: (1) to assess the regeneration niche of Scots pine seedlings following small fires in a dry, inner-alpine valley, and (2) to measure the influence of competition, drought, fertility, and soil pH on pine colonization. We sampled pine seedlings in six high-severity fires (1962-2006), where distance from the unburned edge was <60 m. We modeled seedling density as a function of topography and soil cover by means of Generalized Linear Models (GLM). Ellenberg indicator values (EIV) for light, moisture, soil pH, and fertility were computed from vegetation sampling at each plot, and used as additional predictors of seedling density. Pine colonization was initially slow due to drought, and peaked 16 years after fire. The inclusion of EIV provided +31% of explained deviance in models of seedling density. Herb cover and soil moisture were the most important predictors. Scots pine regenerates successfully following small, high-severity fires, albeit slowly due to unfavorable water balance. Hence, restoration by artificial regeneration may not be necessary when seed dispersal is ensured.

## Keywords

*Ellenberg indicator values; plant diversity; resilience; restoration; wildfire*

Scots pine (*Pinus sylvestris* L.) forests have a wide distribution and ecological amplitude in the northern hemisphere. In the southern Alps, Scots pine behaves as a pioneer species and establishes after disturbances and in abandoned agricultural lands. The only exceptions are dry (rainfall <700 mm year<sup>-1</sup>), inner alpine valleys, where pine is a strong competitor with respect to other conifers, and may form stable communities (Ozenda 1985). These forests are not very productive but provide important ecosystem services (Vacchiano et al. 2008a, 2008b).

Both primary and secondary pine forests in the inner alpine valleys have experienced, in the last decades, high mortality rates related to forest decline (Bigler et al. 2006; Rigling et al. 2012; Vacchiano et al. 2012).

~~Besides~~Additionally, these fire-prone ecosystems have undergone an increase in the frequency and intensity of forest fires, due to both anthropogenic and climatic causes (Zumbrunnen et al. 2009, 2011). Forest restoration is therefore an important ecological and social issue (Beghin et al. 2010).

Lagging or absent Scots pine colonization was observed in mountain regions throughout Southern Europe following large, high-severity wildfires (>300 ha: Retana et al. 2002; Rodrigo et al. 2004; Moser et al. 2010). The main causes have been attributed to: (1) scarce resistance of seeds to the high temperatures attained during intense wildfires (Habrouk et al. 1999), and (2) limited dispersal distance, i.e., <60 m from the parent trees, with the exception of rare, long-distance dispersal events (Debain et al. 2007; Vilà-Cabrera et al. 2012).

On the other hand, contradictory evidence exists regarding Scots pine colonization following small wildfires, i.e., when parent trees are closer than the maximum dispersal distance. In the Alps, there is evidence of both abundant (Beghin et al. 2010, 28 ha fire) and scarce regeneration in fires of comparable size (Kipfer et al. 2011, 2 to 25 ha). Such discrepancies likely result from additional limiting factors

that may or may not be locally important, e.g., poor soil water balance (Oleskog and Sahlén 2000; Castro et al. 2005), competition vs. facilitation by herbs or shrubs (Vickers and Palmer 2000; Nuñez et al. 2003; Hille and Den Ouden 2004), seedling mortality caused by drought or solar radiation (Castro et al. 2004; Moser et al. 2010), or adverse fire effects on micorrhiza (Kipfer et al. 2010; Pérez-Cabello et al. 2010).

Small fires represent a minor part of total area burned in the southern alpine domain, but their frequency is high (Zumbrunnen et al. 2009; Valese et al. 2011), due to fire suppression activities and landscape fragmentation. Conclusive evidence about the abiotic factors that limit Scots pine regeneration following small, high-severity fires (i.e., causing 100% canopy mortality) is needed. Insights into the functional ecology of the species based on field performance of early regeneration (i.e., seedlings) may enhance the success and cost-effectiveness of restoration (Oliet and Jacobs 2012) following commonly occurring fire disturbances in human-impacted mountain regions.

The aims of this paper are (1) to assess vegetation dynamics of the herbaceous, shrub, and tree layers following small high-severity fires in inner-alpine Scots pine forests: the abundance and temporal colonization dynamics of early Scots pine regeneration in dry, inner-alpine Scots pine forests following small high-severity fires, and (2) to assess the relative importance of potential limiting factors, such as site fertility, competition, soil moisture, and soil reaction, on Scots pine regeneration. We used Ellenberg's (1992) indicator values (EIV) as proxies for light intensity, soil moisture, fertility, and pH at each site, with the additional objective of testing whether the inclusion of EIV would improve the accuracy of regeneration models.

Materials and methods

1) Site selection and study area

From a regional database of wildfires in Valle d’Aosta, Italy (source: Corpo Forestale Regione Autonoma Valle d’Aosta, Nucleo Antincendi Boschivi) we selected all fires that occurred in Scots pine forests between 1962 and 2010. In order to control for undesired variability (e.g., Fernandez Calzado et al. 2012), we subsetted the sample to sites similar in elevation (i.e., 1100 to 1600 m a.s.l.), aspect (southerly), fire behavior (crown fire), and post-fire treatment, i.e., salvage logging 1-4 years after fire (Beghin et al. 2010). Between-site variation of other abiotic factors (e.g., soil type, pre-fire forest cover type) was minimized by selecting fires at a maximum distance of 5 km between one another. We also assumed homogeneity of pre-fire understory community based on the proximity of the sites, and on the fact that mature, closed-canopy stands of Scots pine in ecologically similar sites should be associated to homogenous edaphic conditions. The selected fires (N =6) occurred between March and September of their respective year (1962 to 2006). Area burned by crown fire was 41 ha on average. The shape of fire perimeters was such that, in each fire, most of the burned area was <60 m from the unburned edge (Table I). In the two largest fires, we restricted our analysis to a buffer within 60 m from the unburned edge, so that successful seed dispersal was ensured.

(Table I)

~~Burned areas are located in the neighboring municipalities of Verrayes and Saint-Denis.~~ Mean annual precipitation is around 600 mm, and mean annual

temperature is 10° C. Soils are classified as entisols (Beghin et al. 2010). Pine stands belong to the *Ononido-Pinion* alliance (Blasi 2010), that is described as a xerothermic woodland of colline to montane altitudes on alkaline soils, geographically centered on the dry valleys of the inner Alps (Braun-Blanquet 1961; Mucina et al. 1993). The canopy is composed almost exclusively of relatively short Scots pine; *Archtostryphlos uva-ursi* is frequent in the shrub layer (Filipello et al. 1985). In all sites, browsing of the terminal shoots, fraying, and bark stripping by wild ungulates are very rare.

## 2) Data collection

We used individual fires as treatment, similarly to previous research in post-fire regeneration dynamics (Capitanio and Carcaillet 2008; González-Tagle et al. 2008). Lack of true replication is common in wildfire research (Van Mangtem et al. 2001): natural fire is a rare event, and true replicates (i.e., fires of the same age with none or minimal site variation between them) are hard to find. Moreover, in our study the number of wildfire events satisfying the conditions for site selection was very limited.

We randomly established 5 circular plots (radius = 5m) within each fire perimeter, providing a minimum distance of 25 m between plots to avoid spatial autocorrelation, and a maximum distance of 60 m from the unburned forest edge, in order to ensure the arrival of pine seeds dispersed by the wind. Total number of plots was 30. Sampling was carried out in summer 2011. In each plot we measured the following variables:

(a) site: elevation, aspect (subsequently linearized as Heatload Index:

McCune and Keon 2002), percent cover of bare soil, herbaceous, lower



- shrub (height  $\leq 130$  cm, excluding pine seedlings), upper shrub (height between 130 and 500 cm), and tree ( $>500$  cm) layers;
- (b) regeneration: height and root collar diameter (RCD) of all pine seedlings and small saplings (height  $\leq 130$  cm; hereafter, “seedlings”);
- (c) vegetation: presence-absence and visually estimated cover of each species in the herbaceous, lower shrub (excluding pine seedlings), upper shrub, and tree layers. Species with very low cover ( $<1\%$ ) were registered as rare (‘+’), according to Braun-Blanquet (1932). Floristic nomenclature followed Pignatti (1982).

**3) Data analysis**

In order to understand the effect of time since fire on plant succession in the study area, we carried out an indirect gradient analysis (Cárni et al. 2011) of species cover data, by means of nonmetric multidimensional scaling (NMS) with Varimax rotation (Legendre and Legendre 1998). Species with very low cover (‘+’) were assigned using a 0.3% weight (Reichelt and Williams 1973; Tasser and Tappeiner 2005). NMS was run in PCORD 4.17 (McCune and Mefford 1999) with the following configuration: Sorensen distance with Bray-Curtis dissimilarity index, 200 runs with real data, max 250 iterations, stability criterion = 0.0005, random starting configuration, six initial dimensions (McCune and Grace, 2002). Dimensionality was assessed by significance of a Monte-Carlo test (100 runs,  $p \leq 0.05$  where  $p$  = proportion of randomized runs with stress lower or equal than the observed stress). The ecological significance of NMS axes was assessed by Pearson’s correlation with site and soil cover variables.

Ellenberg indicator values for light (~~L~~), moisture (~~U~~), soil reaction, and pH (R), and nutrient content (~~N~~) were associated to each species (Ellenberg et al. 1992, readapted by Pignatti 2005). Mean EIV for the herbaceous and lower shrub layers (excluding pine seedlings) were computed for each plot using both presence-absence (unweighted mean) and percent cover data (weighted mean: Diekmann 2003). We assumed that pine seedlings, having a sparse cover, did not substantially affect the understory, and that current herbaceous and lower shrub composition and abundance at the plot scale was similar to that at the time of seedling emergence.

Following a square-root transformation to ensure normality, we assessed the effect of treatment (i.e., fire year) on pine seedling abundance, total pine cover, and EIV by univariate ANOVA with a Ryan-Einot-Gabriel-Welsch post-hoc test ( $\alpha = 0.05$ ). Finally, in order to assess the influence of limiting factors on Scots pine seedling abundance, we fitted a Generalized Linear Model (GLM) with Poisson error distribution and log link to the following sets of variables: (1) a “reduced” model based on site variables only (i.e., topography and soil cover); (2) a “full” model including topography, site variables, and unweighted EIV; (3) a “full” model including topography, site variables, and weighted EIV. We did not include in our models distance from the unburned edge, because: (a) all plots were within the dispersal range of most Scots pine seeds, i.e., 60 m (Debain et al. 2007); and (b), the oldest post-fire cohorts have already reached sexual maturity (10-20 years in Scots pine: Vilà-Cabrera et al. 2012), and dispersed their seeds to neighboring sites, therefore introducing noise in the variable.

As time since fire was highly correlated to percent tree cover (Pearson's  $R = 0.96$ ), we excluded the first from the set of model predictors. ~~Lower and upper shrub covers were aggregated. In order to improve model parsimony, reduce the~~

number of predictors and avoid model overfitting, we aggregated lower and upper shrub cover. All independent variables were standardized. GLM were assessed for overall significance (omnibus test,  $p \leq 0.05$ ) and compared based on percent deviance explained, Akaike's Information Criterion with small-sample correction (AICC), and Bayesian Information Criterion (BIC). Effect size of individual predictors was assessed by scrutinizing regression coefficients.

Results

1) Temporal vegetation dynamics

A total of 165 plant species were found at all sites; the number of species per plot ranged from 20 to 46. We sampled an average of 38 species (i.e., alpha-diversity) 5 years after fire, and only 24 species 49 years after fire, i.e., a 37% difference ( $p=0.0049$ , heteroschedastic t-test). Mean herbaceous, shrub (lower + upper), and bare soil cover were 60%, 19% and 29% respectively (Table II). Mean EIV were indicative of open, xeric sites with sub-basic soil pH and medium-low fertility. Light decreased and moisture increased with time since fire. N was high in the most recent fire, decreased 16-36 years from fire, and increased again in the oldest fire. R did not show any clear trends (Fig. 1).

(Table I) (Figure 1)

NMS (Fig. 2) suggested an ordination on 3 dimensions (final stress after 250 iterations: 11.49,  $p=0.0099$ ). NMS components (Table III) were mainly

explicative of elevation (axis 1), shrub (axis 2) and tree cover, i.e., time since fire (axis 3).

(Figure 2) (Table III)

Following fire, sprouting broadleaves were the first to recolonize the site (i.e., downy oak *Quercus pubescens*, aspen *Populus tremula*, birch *Betula pendula*, willow *Salix caprea*, ash *Fraxinus excelsior*, cherry *Prunus avium*). Therophytic and nitrophilous early-seral species (e.g., *Crupina vulgaris*, *Medicago minima*, *Tragopogon dubius*, *Daucus carota*), were abundant in the most recent fire, but decreased 6 and 8 years after fire, to the advantage of species from meso-xerophilous shrub and fringe communities (e.g., *Colutea arborescens*, *Amelanchier ovalis*, *Coronilla varia*, *Hypericum perforatum*) and dry grasslands (e.g., *Koeleria pyramidata*, *Centaurea scabiosa*, *Galium verum*, *Lactuca perennis*). Only 16 and 36 years after fire did we observe an increase in species from broadleaved and Scots pine forests (e.g., *Prunus avium*, *Quercus pubescens*, *Astragalus monspessulanus*, *Viola rupestris*). In the oldest site we observed a significant reduction of species from dry grasslands, and the appearance of species from boreal acidophilous woody communities (e.g., *Picea excelsa*, *Melampyrum sylvaticum*, *Vaccinium myrtillus*).

## 2) Pine regeneration

The density of Scots pine seedlings ranged from none in the most recent fire, to an average of 1900 seedlings ha<sup>-1</sup> in the 1995 fire. While seedling density declined in older fires, the cover of pine regeneration of all ages continued to increase, up to

an average 61% in the oldest site, 49 years after fire (Fig. 3).

(Figure 3)

**3) Limiting factors to pine regeneration**

All regeneration models were significant (omnibus test,  $p < 0.001$ ). Deviance explained improved from 57% (reduced model) to 88% when using EIV as additional predictors (Table IV). ‘Full’ models had similar deviance explained, AICC, and BIC (i.e., less than 2 units apart). However, the set of significant model parameters (Table V) differed.

In the reduced model, all site variables were significant, and positively related to seedling abundance. When using the uweighted EIV model, we observed a significant influence of moisture ( $b = 2.40$ ), soil reaction ( $b = 2.40$ ), and soil fertility ( $b = -1.96$ ), and a weaker, positive effect of herbaceous cover ( $b = 1.67$ ) and heatload ( $b = 0.44$ ). In the weighted EIV model herb cover, bare soil cover, and light intensity were the most important predictors ( $b = 3.14$ ,  $-2.16$  and  $2.13$ , respectively); a positive effect of total shrub cover ( $b = 1.44$ ) and heatload ( $b = 1.3$ ), and a negative effect of tree cover ( $b = -1.79$ ), were also observed.

(Table IV) (Table V)

## Discussion

### 1) Temporal vegetation dynamics

In the first years after fire, we observed the dominance of ruderal nitrophilous therophytes and perennial communities (*Thero-Brachypodietea*, *Stellarietea mediae*, *Agropyreteae intermedii-repentis* and *Artemisietea vulgaris* classes). Within these classes, drought-resistant species such as *Conyza canadensis* or *Lactuca serriola* were observed, similarly to observations in other dry, inner-alpine valleys (Moser and Wohlgemuth 2006), as a likely result of high solar radiation and strong water deficit.

With increasing time since fire, a transition was observed towards perennial species of xerophytic grasslands and forest ~~edges-ecotones~~ (*Festuco-Brometea* and *Crataego-Prunetea*). Species from *Pyrolo-Pinetetia* (i.e., Scots pine and related species) and *Quercus-Fagetetia* s.l. appeared ~~only at a second stage~~ later in the succession, i.e., 15 years after fire.

In the oldest fires (36 and 49 years since fire), we observed the appearance of *Vaccinio-Picetia* species (i.e., *Picea* and related herbaceous species), consistently with their shade-tolerance traits, and preference for fertile soils (Hofgaard 1993). Ordination analysis confirmed that this succession of plant communities was mainly associated with the increase in tree canopy cover.

### 2) Pine regeneration

Pine seedlings were absent from the most recent fire (5 years since fire), peaked 16 years after fire, and declined in the oldest fires. Scarce regeneration of Scots pine in the first years after fire has been observed both in the Mediterranean

region (Rodrigo et al. 2004) and in the Alps (Moser et al. 2010). Scots pine is characterized by non-serotinous cones, absence of hard-coated seeds, and short-to-medium seed dispersal distances (Vilà-Cabrera et al. 2012). Once burned in an intense fire, it is dependent for recovery on seed dispersal from adjacent unburned patches (Ramon Vallejo et al. 2012). For this reason, large, high-severity fires may delay regeneration by many years (Rodrigo et al. 2004; see also Turner et al. 1998).

Dispersal distance was not limiting in our study. However, the most favorable time for seedling establishment was 8 to 16 years after fire, i.e., a later (and longer) window than that found in Mediterranean ecosystems (Retana et al. 2012). Although Scots pine is a light-demanding species, seed germination and seedling survival are very sensitive to drought (Castro et al. 2005), especially in inner alpine sites, where spring and summer precipitation are scarce (Moser et al. 2010). It is likely that the extremely unfavorable soil water balance, especially during summer, has resulted in a particularly slow establishment. Once herbs and shrubs are established, however, they may act as nurse plants, buffering summer drought without reducing radiation to critical levels, as was previously observed in similar environments (Castro et al. 2004, Pardos et al. 2007).

In the older sites, pines that had established after fire have formed a closed canopy and entered a competitive exclusion phase (Oliver and Larson 1996; Vacchiano et al. 2008b). Following canopy closure and self-thinning of the main cohort, scarce or no new seedlings could establish in the understory, due to limiting light conditions. No shift in dominant tree species was observed, as had by contrast been predicted following large fires in dry Mediterranean and Alpine sites (Moser et al. 2010; Vilà-Cabrera et al. 2012). ~~As we expected, we found few or no seedlings in these sites, because of the denser tree cover.~~

### 3) Limiting factors to pine regeneration

Regeneration models that included EIV had a better fit, indicating a significant influence of microsite conditions. Unweighted EIV produced slightly better models, and three out of four EIV were significant only when computed from presence/absence data. Previous research suggested that presence/absence data are more responsive to environmental variation than abundance data (Smartt et al. 1976; Wilson 2012). Unweighted EIV attribute a greater importance to sporadic species with high indicator power, in our case, mesophilous species that contrast with the general dryness of the area (e.g., *Fraxinus excelsior*, *Viola riviniana*, *Lathyrus montanus*). Site predictors, on the other hand, were more significant in the reduced model, likely because they captured the variability in the response that was not explained by the EIV.

The effect of model predictors was consistent with our hypotheses: a) tree cover always had a negative effect on seedling abundance, as expected for a light-demanding species such as Scots pine; b) heatload had a positive influence on pine establishment, but ~~direct solar radiation (L)~~light was strongly limiting. This is expected in drought-prone sites, where the evapotranspiration balance is negative (Braun-Blanquet 1961, Schwabe and Kratochwil 2004); c) moisture was the strongest predictor (in the unweighted model), with higher moisture resulting in denser pine regeneration; d) herbaceous and shrub cover (when significant) were positively associated with pine density, indicating a potential facilitative effect played out by alleviating drought and evapotranspiration at ground level. ~~pH~~Soil reaction was significant in the unweighted EIV model only. Soils were homogenous across sites- However, litterfall from established pine trees can



increase topsoil acidity in the oldest fires, and Scots pine seedlings reportedly have a limited ability to cope with water limitations in more acidic soils (Bartsch 1987). However, this EIV is less reliable when used in young secondary forests (Dzwonko 2001).

Finally, site fertility had a strong, negative effect on pine seedling abundance. Scots pine is known to thrive on poorer soils (as confirmed by the positive effect of bare soil cover in the weighted model), and to be a poor competitor when site resources are more abundant (Picon-Cochard et al. 2006). N was high both in the most recent fire (post-fire fertilization: Maringer et al. 2011) and in the oldest one, likely due to litter accumulation. In these same sites, pine seedlings were scarce, even if mostly limited by U-moisture and lightL, respectively.

In conclusion, our study showed that even after small, high-severity fires, pine establishment is initially slow in dry, inner-alpine Valle d'Aosta (Italy), due to the unfavorable moisture regime and evapotranspiration balance. Seedling density increased with time since fire, peaked between 8 and 16 years after fire, and subsided in older fires, where post-fire trees represented the mature canopy. Contrary to larger fires, where a change in dominant species may occur because of seed dispersal limitations, pine finally achieved dominance. This indicates that Scots pine is capable, despite drought limitations, to colonize small areas burned by high-severity fire, albeit slowly. The fact has clear management implications: if such a large temporal lag is tolerable (e.g., not in direct protection forests, where the fastest recovery of plant cover is desired to mitigate natural hazards), small-sized fires and areas surrounding unburned edges can be safely left to develop according to their natural dynamics, in contrast to larger fires, where planting may be needed for effective restoration. Moreover, the facilitative effect of herbs and shrubs indicates-confirmed that they are key microhabitats in the

early phase of post-fire establishment in dry, inner-alpine Scots pine forests-  
(Castro et al. 2004).

## Acknowledgements

We acknowledge Diego Trucchi for field sampling, James N. Long for language review, Raffaella Marzano, Emanuele Lingua and Matteo Garbarino for ideas and discussion, and Davide Ascoli for wildland fire expertise. Project funded by the trans-boundary cooperation programme Alcotra 2007-2013 - Project 32: "Foreste di protezione: tecniche gestionali e innovazione nelle Alpi occidentali".

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## Tables

**Table I** Characteristics of the selected fires

Year	Site	Latitude Longitude (WGS84)	Area burned by crown fire [ha]	Area within 60m from fire edge [ha (%)]	Elevation range of crown fire [m a.s.l.]	Aspect
1962	Lavasè	45°45'54"N 7°34'57"E	5.4	5.4 (100%)	1490-1550	SW
1975	Chialey	45°46'16"N 7°32'36"E	2.1	2.1 (100%)	1245-1335	S
1995	Del	45°46'19"N 7°33'15"E	22.0	21.9 (99.4%)	1160-1460	S
2003	Vorpeillere	45°45'40"N 7°35'06"E	46.4	35.4 (76.2%)	970-1525	SE
2005	Hers	45°46'10"N 7°29'54"E	167.9	74.2 (44.2%)	1305-1890	S
2006	Menfrey	45°46'00"N 7°30'50"E	4.6	4.5 (99.3%)	1020-1340	SE

**Table II** Plot-scale descriptors (N =30) of regeneration, site, soil cover variables, EIV (unweighted and weighted), and number of species per plot (i.e., alpha-diversity). ~~L: light intensity; U: moisture; N: fertility; R: pH~~

		Units	Mean	SE	Min	Max
Scots pine regeneration	<i>Pine seedling density</i>	trees ha <sup>-1</sup>	425.9	142.7	0	2801
Site variables	<i>Elevation</i>	m a.s.l.	1306.7	23.84	1117	1559
	<i>Heatload</i>	(0-1)	0.30	0.02	0.0	0.5
	<i>Herbaceous</i>	%	60.2	3.03	20	85
	<i>Tree cover</i>	%	22.4	5.54	0	75
	<i>Lower shrub cover</i>	%	9.2	1.67	0	30
	<i>Upper shrub cover</i>	%	9.9	1.79	0	35
	<i>Bare soil</i>	%	29.3	3.99	3	72
EIV, unweighted	<del>Light</del>	1-9	7.4	0.095	6.4	8.5
	<del>Moisture</del> U	1-12	3.5	0.051	3.0	4.2
	<del>Soil reaction</del> R	1-9	6.7	0.084	5.3	7.2
	<del>Nutrients</del>	1-9	3.2	0.064	2.4	3.9
EIV, weighted	<del>Light</del>	1-9	7.3	0.114	6.3	8.3
	<del>Moisture</del> U	1-12	3.5	0.073	2.7	4.4
	<del>Soil reaction</del> R	1-9	7.1	0.070	6.3	7.8
	<del>Nutrients</del>	1-9	3.3	0.114	2.1	4.7
<i>Number of species</i>		-	33.8	1.32	20	46

**Table III** Pearson's correlation coefficientbetween site variables and NMS axes. \* $p \leq 0.05$ ,\*\* $p \leq 0.01$ , \*\*\* $p \leq 0.001$ 

Variable	NMS 1	NMS 2	NMS 3
Elevation	-0.67***	0.16	-0.35
Heatload	-0.19	0.05	-0.34
Tree cover	-0.52**	-0.25	-0.77***
Lower shrub cover	-0.05	0.02	0.13
Upper shrub cover	-0.22	-0.35	0.23
Herbaceous	0.10	0.01	0.09
Bare soil	-0.18	-0.25	-0.39*



**Table IV** GLM fit statistics for Scots pine seedling abundance (N). Df: degrees of freedom; LL: Log Likelihood; AICC: Finite Sample Corrected AIC; BIC: Bayesian Information Criterion

Response variable	Null deviance	Predictors	df	Residual deviance	% Deviance explained	LL	AICC	BIC
N	245.9	Site	23	106.6	56.6%	-75.9	170.8	175.5
		Site, EIV unweighted	19	29.6	88.0%	-37.4	111.4	112.1
		Site, EIV weighted	19	30.4	87.6%	-37.8	112.2	113.0

**Table V** Coefficients (b) and significance (sig.) of predictors in GLM of Scots pine seedling abundance.

Model and predictors	b	sig.
Site		
(Intercept)	-0.34	0.285
Elevation	1.35	0.000
Heatload	0.60	0.001
Tree cover	0.88	0.000
Total shrub cover	0.88	0.000
Herbaceous	2.65	0.000
Bare soil	1.37	0.011
Site, EIV unweighted		
(Intercept)	-0.75	0.056
Elevation	-0.44	0.533
Heatload	0.44	0.050
Tree cover	-0.86	0.199
Total shrub cover	-0.38	0.361
Herbaceous	1.67	0.027
Bare soil	0.41	0.576
<del>Light</del>	-1.65	0.059
<del>Moisture</del>	2.40	0.000
<del>Soil reaction</del>	2.04	0.000
<del>Nutrients</del>	-1.96	0.000
Site, EIV weighted		
(Intercept)	-1.74	0.019
Elevation	0.88	0.146
Heatload	1.30	0.000
Tree cover	-1.79	0.010
Total shrub cover	1.44	0.008
Herbaceous	3.14	0.003
Bare soil	2.16	0.045
<del>Light</del>	-2.13	0.000
<del>Moisture</del>	0.04	0.956
<del>Soil reaction</del>	0.32	0.440
<del>Nutrients</del>	-1.79	0.056

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Legends to figures

**Fig. 1** Unweighted (left) and weighted (right) average EIV in the 6 fires selected. Error bars represent standard error. Letters from ANOVA with post-hoc REGW Q test ( $\alpha=0.95$ )

**Fig. 2** NMS ordination of species composition and fire years (centroids of 5 plots per site), biplot of axes 1-2 [A] and 1-3 [B]. Species codes: Aab: *Artemisia absinthium*. Aag: *Alyssum argenteum*. Aal: *Ailanthus altissima*. Aar: *Acinos arvensis*. Aay: *Alyssum alyssoides*. Aca: *Achnatherum calamagrostis*. Ach: *Ajuga chamaepitys*. Acm: *Artemisia campestris*. Aco: *Achillea collina*. Adi: *Antennaria dioica*. Agl: *Arabis glabra*. Ahi: *Arabis hirsuta*. Ali: *Anthericum liliago*. Amo: *Astragalus monspessulanus*. Ano: *Achillea nobilis*. Aon: *Astragalus onobrychis*. Aov: *Amelanchier ovalis*. Apy: *Ajuga pyramidalis*. Aru: *Asplenium ruta-muraria*. Auv: *Arctostaphylos uva-ursi*. Avl: *Artemisia vulgaris*. Avu: *Anthyllis vulneraria* subsp. *polyphylla*. Ber: *Bromus erectus*. Bla: *Biscutella laevigata*. Bpe: *Betula pendula*. Bra: *Bupleurum ranunculoides*. Bru: *Brachypodium rupestre*. Bvu: *Berberis vulgaris*. Cab: *Colutea arborescens*. Cal: *Chenopodium album*. Cap: *Clematis alpina*. Car: *Cirsium arvense*. Cav: *Convolvulus arvensis*. Cca: *Conyza canadensis*. Cer: *Cirsium eriophorum*. Cgr: *Chrysopogon gryllus*. Chu: *Carex humilis*. Cmi: *Chaenorhinum minus*. Cnu: *Carduus nutans*. Cro: *Campanula rotundifolia*. Csc: *Centaurea scabiosa*. Ctr: *Centaurea triumfetti*. Cut: *Carlina utzka*. Cva: *Calamagrostis varia*. Cvi: *Clematis vitalba*. Cvl: *Crupina vulgaris*. Cvr: *Coronilla varia*. Cvu: *Carlina vulgaris*. Dea: *Daucus carota*. Dte: *Diplotaxis tenuifolia*. Eac: *Erigeron acer*. Ean: *Epilobium angustifolium*. Eat: *Epipactis atropurpurea*. Eau: *Erigeron annuus*. Eca: *Eryngium campestre*. Ecy: *Euphorbia cyparissias*. Ena: *Erucastrum nasturtiifolium*. Erh: *Erysimum rhaeticum*. Ese: *Euphorbia seguierana*. Evu: *Echium vulgare*. Far: *Festuca arundinacea*. Fci: *Festuca cinerea*. Fex: *Fraxinus excelsior*. Fpr: *Fumana procumbens*. Fva: *Festuca valesiaca*. Fve: *Fragaria vesca*. Gap: *Galium aparine*. Gcn: *Gymnadenia conopsea*. Gco: *Galium corrudifolium*. Gve: *Galium verum*. Hco: *Hippocrepis comosa*. Hfo: *Helleborus foetidus*. Hnu: *Helianthemum nummularium* subsp. *obscurum*. Hpe: *Hieracium peletierianum*. Hpi: *Hieracium piloselloides*. Hpr: *Hypericum perforatum*. Hsy: *Hieracium sylvaticum*. Hto: *Hieracium tomentosum*. Ico: *Inula conyza*. Jco: *Juniperus communis*. Kpy: *Koeleria pyramidata*. Ksa: *Kernera saxatilis*. Kva: *Koeleria vallesiana*. Lco: *Leopoldia comosa*. Lcr: *Lotus corniculatus*. Lde: *Larix decidua*. Lhi: *Leontodon hispidus*. Lmo: *Lathyrus montanus*. Lpe: *Lactuca perennis*. Lse: *Lactuca serriola*. Lsi: *Laserpitium siler*. Lsm: *Linaria simplex*. Lvu: *Ligustrum vulgare*. Mci: *Melica ciliata*. Mfa: *Medicago sativa* subsp. *falcata*. Mfs: *Minuartia fastigiata*. Mlu: *Medicago lupulina*. Mmi: *Medicago minima*. Mof: *Melilotus officinalis*. Msa: *Medicago sativa* subsp. *sativa*. Msy: *Melampyrum sylvaticum*. Oca: *Orobanche caryophyllacea*. Oha: *Oxytropis halleri*. Ola: *Odontites lanceolata*. Olu: *Odontites lutea*. Ona: *Ononis natrix*. Opi: *Oxytropis pilosa*. Opu: *Ononis pusilla*. Ore: *Ononis repens*. Oro: *Ononis rotundifolia*. Ovi: *Onobrychis viciifolia*. Pav: *Prunus avium*. Pch: *Polygala chamaebuxus*. Pex: *Picea excelsa*. Pgr: *Prunella grandiflora*. Phi: *Picris hieracioides*. Pma: *Prunus mahaleb*. Pni: *Populus nigra*. Por: *Peucedanum oreoselinum*. Ppa: *Poa pratensis*. Pph: *Phleum phleoides*. Ppr:

*Petrorhagia prolifera*. Psa: *Petrorhagia saxifraga*. Psp: *Prunus spinosa*. Psx: *Pimpinella saxifraga*. Psy: *Pinus sylvestris*. Pta: *Potentilla tabernaemontani*. Ptr: *Populus tremula*. Pun: *Pinus uncinata*. Qpu: *Quercus pubescens*. Rca: *Rosa canina*. Rid: *Rubus idaeus*. Rul: *Rubus spp.* Sar: *Sorbus aria*. Sca: *Salix caprea*. Sgr: *Scabiosa gramuntia*. Sin: *Senecio inaequidens*. Sit: *Silene italica*. Smi: *Sanguisorba minor*. Smo: *Sedum montanum*. Snu: *Silene nutans*. Soc: *Saponaria ocymoides*. Sot: *Silene otites*. Spe: *Stipa pennata*. Spr: *Salvia pratensis*. Sre: *Stachys recta*. Ste: *Sempervivum tectorum*. Tch: *Teucrium chamaedrys*. Tcr: *Tragopogon crocifolius*. Tdu: *Tragopogon dubius*. Thu: *Thymus humifusus*. Tla: *Taraxacum laevigatum*. Tli: *Thesium linophyllum*. Tme: *Trifolium medium*. Tmo: *Teucrium montanum*. Tof: *Taraxacum officinale*. Tvu: *Thymus vulgaris*. Var: *Viola arvensis*. Vly: *Verbascum lychnitis*. Vmy: *Vaccinium myrtillus*. Vof: *Veronica officinalis*. Vri: *Viola riviniana*. Vru: *Viola rupestris*. Vsa: *Vicia sativa*. Vth: *Verbascum thapsus*

**Fig. 3** Average seedling density (white bars) and average percent cover by the shrub and tree layers (grey bars) for Scots pine in the 6 fires selected. Error bars represent SE. Letters from ANOVA with post-hoc REGW Q test ( $\alpha=0.95$ )

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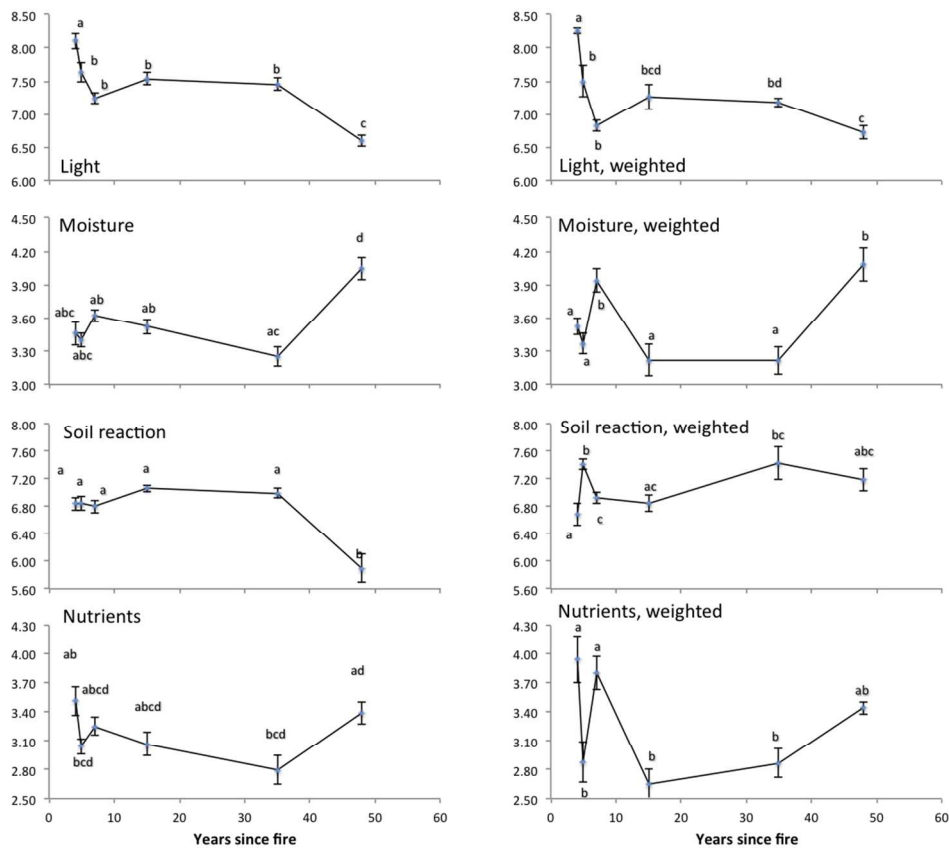
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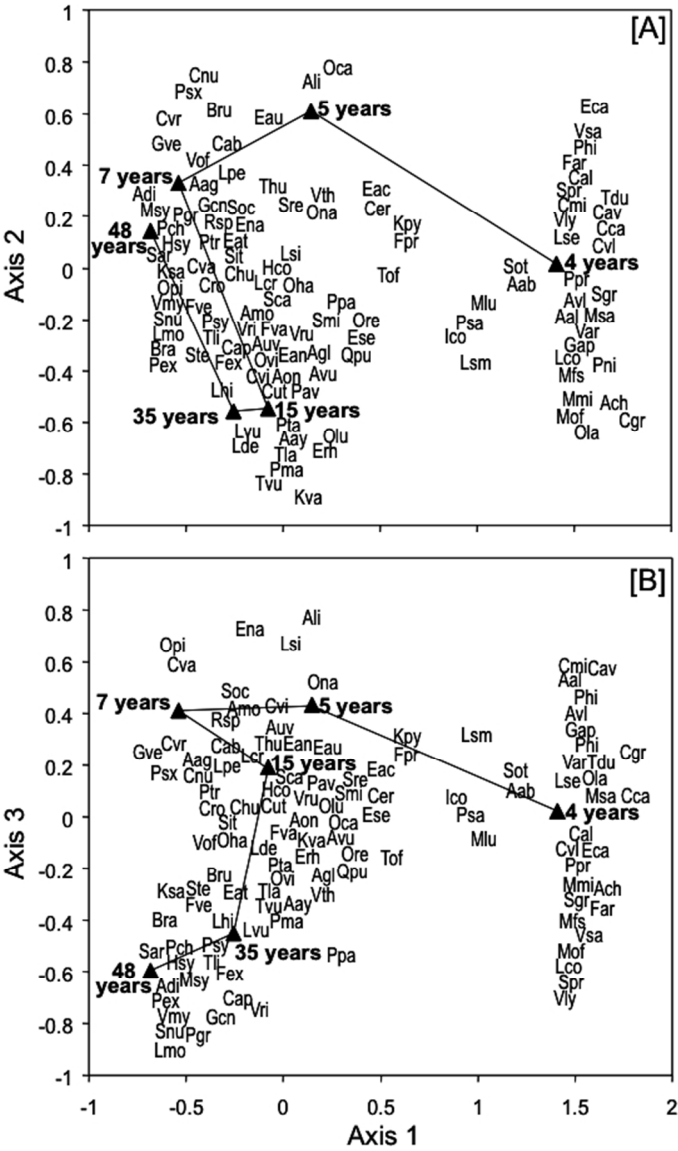
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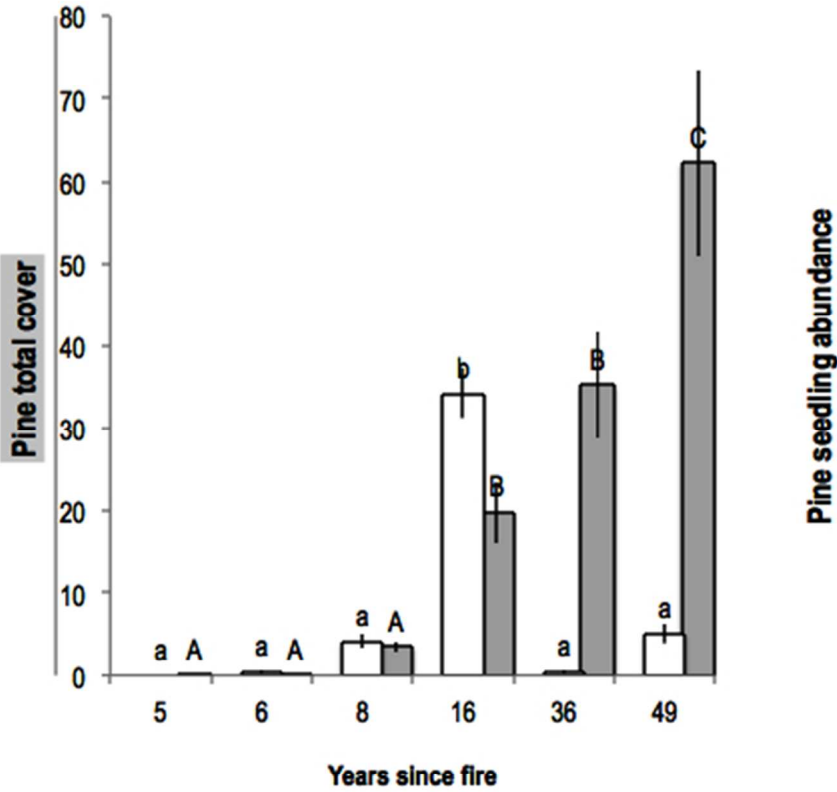


Unweighted (left) and weighted (right) average EIV in the 6 fires selected. Error bars represent standard error. Letters from ANOVA with post-hoc REGW Q test ( $\alpha = 0.95$ )

414x351mm (72 x 72 DPI)



NMS ordination of species composition and fire years (centroids of 5 plots per site), biplot of axes 1-2 [A] and 1-3 [B]  
254x338mm (72 x 72 DPI)



Average seedling density (white bars) and average percent cover by the shrub and tree layers (grey bars) for Scots pine in the 6 fires selected. Error bars represent SE. Letters from ANOVA with post-hoc REGW Q test (alpha =0.95)  
162x161mm (72 x 72 DPI)



Code	Species name	Phytosociological optimum (Aeschimann et al. 2004)	Occurrence in 5 samples (min/max % cover)					
			4 years after fire	5 years after fire	7 years after fire	15 years after fire	35 years after fire	48 years after fire
Agropyreteae intermedii-repentis and subordinated units								
Cav	<i>Convolvulus arvensis</i>	<i>Convolvulo-Agropyron repentis</i>	2 (+/3)	0	0	0	0	0
Msa	<i>Medicago sativa</i> ssp. <i>sativa</i>	<i>Agropyreteae intermedii-repentis</i>	2 (+/+)	0	0	0	0	0
Tdu	<i>Tragopogon dubius</i>	<i>Convolvulo-Agropyron repentis</i>	2 (+/1)	0	0	0	0	0
Artemisietea vulgaris and subordinated units								
Agl	<i>Arabis glabra</i>	<i>Geo-Alliarion</i>	0	1 (+/+)	0	0	3 (+/+)	0
Aab	<i>Artemisia absinthium</i>	<i>Onopordetalia acanthii</i>	5 (6/28)	4 (+/10)	2 (+/2)	4 (+/4)	1 (+/+)	0
Avl	<i>Artemisia vulgaris</i>	<i>Artemisietea vulgaris</i>	1 (+/+)	0	0	0	0	0
Cnu	<i>Carduus nutans</i>	<i>Onopordetalia acanthii</i>	0	0	1 (2/2)	0	0	0
Cer	<i>Cirsium eriophorum</i>	<i>Onopordetalia acanthii</i>	4 (+/1)	3 (+/+)	4 (+/1)	1 (+/+)	1 (+/+)	1 (+/+)
Dca	<i>Daucus carota</i>	<i>Dauco-Melilotion</i>	5 (1/13)	0	0	1 (1/1)	0	0
Eau	<i>Erigeron annuus</i>	<i>Artemisietea vulgaris</i>	0	1 (+/+)	1 (+/+)	0	0	0
Gap	<i>Galium aparine</i>	<i>Galio-Alliaretalia</i>	1 (+/+)	0	0	0	0	0
Lse	<i>Lactuca serriola</i>	<i>Onopordetalia acanthii</i>	5 (+/3)	0	0	2 (+/+)	0	0
Mof	<i>Melilotus officinalis</i>	<i>Dauco-Melilotion</i>	2 (+/3)	0	0	0	0	0
Phi	<i>Picris hieracioides</i> subsp. <i>hieracioides</i>	<i>Dauco-Melilotion</i>	2 (1/3)	0	0	0	0	0
Sin	<i>Senecio inaequidens</i>	<i>Artemisietea vulgaris</i>	2 (+/6)	3 (+/6)	5 (+/10)	1 (+/+)	0	0
Asplenietea trichomanis and subordinated units								
Aag	<i>Alyssum argenteum</i>	<i>Asplenion serpentine</i>	0	0	1 (+/+)	0	0	0
Aru	<i>Asplenium ruta-muraria</i>	<i>Potentilletalia caulescentis</i>	0	0	0	0	0	1 (+/+)
Hto	<i>Hieracium tomentosum</i>	<i>Potentillion caulescentis</i>	0	1 (+/+)	0	0	0	0
Ksa	<i>Kernera saxatilis</i>	<i>Potentilletalia caulescentis</i>	0	0	0	0	0	1 (+/+)
Carpino-Fagetea sylvaticae and subordinated units								
Fex	<i>Fraxinus excelsior</i>	<i>Carpino-Fagetea sylvaticae</i>	0	0	0	0	2 (+/+)	2 (+/+)
Hsy	<i>Hieracium sylvaticum</i>	<i>Carpino-Fagetea sylvaticae</i>	0	1 (+/+)	2 (+/+)	0	2 (+/1)	5 (2/6)
Pni	<i>Populus nigra</i>	<i>Populetalia albae</i>	1 (1/1)	0	0	0	0	0
Pav	<i>Prunus avium</i>	<i>Carpinion betuli</i>	0	1 (+/+)	0	3 (+/+)	1 (+/+)	0
Crataego-Prunetea and subordinated units								
Aov	<i>Amelanchier ovalis</i>	<i>Berberidenion</i>	0	1 (+/+)	0	0	0	0
Bvu	<i>Berberis vulgaris</i>	<i>Berberidenion vulgaris</i>	3 (1/8)	5 (2/8)	2 (+/2)	0	2 (+/2)	0
Cvi	<i>Clematis vitalba</i>	<i>Crataego-Prunetea</i>	1 (1/1)	0	0	3 (+/6)	0	0
Jco	<i>Juniperus communis</i>	<i>Prunetalia spinosae</i>	0	0	0	0	2 (3/5)	1 (+/+)
Lvu	<i>Ligustrum vulgare</i>	<i>Prunetalia spinosae</i>	0	0	0	0	2 (+/1)	0
Pma	<i>Prunus mahaleb</i>	<i>Berberidenion</i>	1 (+/+)	0	0	2 (+/+)	5 (+/2)	0
Psp	<i>Prunus spinosa</i>	<i>Prunetalia spinosae</i>	0	0	0	0	2 (20/30)	0
Rca	<i>Rosa canina</i>	<i>Prunetalia spinosae</i>	4 (1/8)	2 (2/4)	0	4 (+/1)	4 (+/+)	2 (+/+)
Rid	<i>Rubus idaeus</i>	<i>Sambuco-Salicion capreae</i>	0	3 (+/4)	3 (+/3)	1 (+/+)	0	3 (+/2)
Rul	<i>Rubus ulmifolius</i>	<i>Crataego-Prunetea</i>	0	0	5 (10/20)	5 (1/6)	3 (+/5)	3 (+/3)
Sca	<i>Salix caprea</i>	<i>Sambuco-Salicion capreae</i>	1 (+/+)	2 (1/3)	3 (5/5)	3 (3/8)	0	3 (1/5)
Elyno-Seslerietea varia and subordinated units								
Bla	<i>Biscutella laevigata</i>	<i>Seslerion varia</i>	0	1 (+/+)	1 (+/+)	0	0	0
Bra	<i>Bupleurum ranunculoides</i>	<i>Seslerion varia</i>	0	0	0	0	0	1 (+/+)
Ean	<i>Epilobium angustifolium</i>	<i>Epilobion angustifolii</i>	3 (+/+)	3 (+/1)	3 (+/+)	5 (1/6)	0	1 (+/+)
Fve	<i>Fragaria vesca</i>	<i>Epilobietea angustifolii</i>	2 (+/+)	1 (+/+)	2 (+/+)	4 (1/6)	1 (+/+)	5 (1/10)

Vth	<i>Verbascum thapsus</i>	<i>Atropion</i>	0	2 (+/+)	0	0	2 (+/+)	0
<i>Erico-Pinetea</i> and subordinated units								
Cva	<i>Calamagrostis varia</i>	<i>Erico-Pinetalia</i>	0	1 (+/+)	3 (+/29)	0	0	1 (1/1)
Eat	<i>Epipactis atropurpurea</i>	<i>Erico-Pinetea</i>	1 (+/+)	3 (+/1)	2 (+/+)	1 (+/+)	0	5 (+/2)
Pch	<i>Polygala chamaebuxus</i>	<i>Erico-Pinetea</i>	0	0	3 (2/2)	0	1 (+/+)	5 (15/26)
<i>Festuco-Brometea</i> and subordinated units								
Aco	<i>Achillea collina</i>	<i>Festucetalia valesiacae</i>	5 (1/6)	0	0	0	1 (+/+)	0
Ano	<i>Achillea nobilis</i>	<i>Festuco-Brometea</i>	3 (+/1)	1 (+/+)	1 (+/+)	4 (+/2)	1 (+/+)	1 (+/+)
Ali	<i>Anthericum liliago</i>	<i>Festuco-Brometea</i>	0	1 (+/+)	0	0	0	0
Avu	<i>Anthyllis vulneraria</i> subsp. <i>polyphylla</i>	<i>Festuco-Brometea</i>	1 (+/+)	0	1 (+/+)	3 (+/+)	1 (+/+)	0
Ahi	<i>Arabis hirsuta</i>	<i>Festuco-Brometea</i>	0	0	0	0	0	1 (+/+)
Acm	<i>Artemisia campestris</i>	<i>Festuco-Brometea</i>	4 (+/1)	0	0	0	1 (+/+)	0
Aon	<i>Astragalus onobrychis</i>	<i>Festucetalia valesiacae</i>	2 (+/+)	4 (+/2)	0	5 (+/6)	5 (+/3)	0
Bru	<i>Brachypodium rupestre</i>	<i>Festuco-Brometea</i>	0	5 (1/26)	5 (1/28)	1 (+/+)	1 (3/3)	5 (6/52)
Ber	<i>Bromus erectus</i>	<i>Brometalia erecti</i>	2 (+/26)	1 (+/+)	0	2 (+/+)	4 (6/30)	0
Cro	<i>Campanula rotundifolia</i>	<i>Mesobromion</i>	0	3 (+/+)	3 (+/+)	3 (+/2)	2 (+/+)	3 (+/+)
Chu	<i>Carex humilis</i>	<i>Festuco-Brometea</i>	1 (+/+)	5 (1/15)	5 (6/26)	5 (3/15)	5 (3/15)	5 (6/26)
Cut	<i>Carlina utzka</i>	<i>Ononidetalia striatae</i>	0	0	0	2 (+/1)	1 (+/+)	0
Cvu	<i>Carlina vulgaris</i>	<i>Brometalia erecti</i>	0	0	0	5 (+/4)	0	0
Csc	<i>Centaurea scabiosa</i>	<i>Festuco-Brometea</i>	2 (+/1)	4 (+/4)	2 (+/+)	0	1 (+/+)	0
Cgr	<i>Chrysopogon gryllus</i>	<i>Scorzonero-Chrysopogonetalia</i>	1 (+/+)	0	0	0	0	0
Eac	<i>Erigeron acer</i>	<i>Festuco-Brometea</i>	3 (+/+)	5 (+/+)	2 (+/+)	1 (+/+)	0	0
Eca	<i>Eryngium campestre</i>	<i>Festuco-Brometea</i>	1 (1/1)	0	0	0	0	0
Erh	<i>Erysimum rhaeticum</i>	<i>Festuco-Brometea</i>	1 (+/+)	0	0	4 (+/+)	3 (+/1)	0
Ecy	<i>Euphorbia cyparissias</i>	<i>Festuco-Brometea</i>	0	5 (+/6)	3 (+/+)	0	2 (+/+)	3 (+/+)
Ese	<i>Euphorbia seguierana</i>	<i>Festucetalia valesiacae</i>	1 (+/+)	2 (+/+)	0	1 (1/1)	1 (+/+)	0
Fci	<i>Festuca cinerea</i>	<i>Ononidetalia striatae</i>	0	0	0	1 (1/1)	3 (+/2)	2 (+/+)
Fva	<i>Festuca valesiaca</i>	<i>Festucetalia valesiacae</i>	0	1 (+/+)	0	1 (+/+)	1 (+/+)	0
Fpr	<i>Fumana procumbens</i>	<i>Festuco-Brometea</i>	4 (+/5)	5 (+/6)	1 (+/+)	2 (+/8)	2 (+/+)	0
Gco	<i>Galium corrudifolium</i>	<i>Festuco-Brometea</i>	1 (+/+)	2 (1/6)	1 (+/+)	2 (+/+)	4 (+/3)	0
Gve	<i>Galium verum</i>	<i>Festuco-Brometea</i>	0	0	4 (+/6)	0	0	3 (+/+)
Hnu	<i>Helianthemum nummularium</i> subsp. <i>obscurum</i>	<i>Festuco-Brometea</i>	4 (+/15)	3 (1/6)	2 (1/1)	1 (+/+)	5 (+/+)	0
Hco	<i>Hippocrepis comosa</i>	<i>Festuco-Brometea</i>	2 (+/+)	4 (1/10)	5 (+/6)	4 (2/15)	5 (+/1)	1 (+/+)
Kpy	<i>Koeleria pyramidata</i>	<i>Brometalia erecti</i>	3 (+/1)	1 (2/2)	0	1 (+/+)	1 (+/+)	0
Kva	<i>Koeleria valesiana</i>	<i>Ononidetalia striatae</i>	0	1 (+/+)	0	2 (1/10)	5 (+/2)	1 (+/+)
Lpe	<i>Lactuca perennis</i>	<i>Festuco-Brometea</i>	0	0	1 (+/+)	0	0	0
Mlu	<i>Medicago lupulina</i>	<i>Festuco-Brometea</i>	4 (+/1)	0	0	1 (+/+)	2 (+/+)	0
Mci	<i>Melica ciliata</i>	<i>Festuco-Brometea</i>	5 (1/15)	3 (+/+)	0	5 (+/26)	0	0
Olu	<i>Odontites lutea</i>	<i>Festuco-Brometea</i>	0	0	0	4 (+/1)	1 (+/+)	0
Ovi	<i>Onobrychis viciifolia</i>	<i>Mesobromion</i>	2 (+/+)	1 (+/+)	0	0	2 (1/3)	0
Ona	<i>Ononis natrix</i>	<i>Festuco-Brometea</i>	3 (1/2)	1 (1/1)	2 (2/6)	0	0	0
Opu	<i>Ononis pusilla</i>	<i>Ononidetalia striatae</i>	5 (+/5)	4 (+/1)	2 (+/2)	3 (+/3)	0	0
Ore	<i>Ononis repens</i>	<i>Mesobromion</i>	3 (1/10)	3 (+/2)	1 (6/6)	5 (3/10)	5 (+/8)	0
Oca	<i>Orobancha caryophyllacea</i>	<i>Festuco-Brometea</i>	0	1 (+/+)	0	0	0	0
Oha	<i>Oxytropis halleri</i>	<i>Festucetalia valesiacae</i>	0	3 (+/+)	0	3 (+/+)	1 (+/+)	0
Opi	<i>Oxytropis pilosa</i>	<i>Festucetalia valesiacae</i>	0	0	2 (+/1)	0	0	0
Pph	<i>Phleum phleoides</i>	<i>Festuco-Brometea</i>	2 (1/2)	0	0	1 (+/+)	4 (+/3)	0

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Psx	<i>Pimpinella saxifraga</i>	<i>Festuco-Brometea</i>	0	0	1 (1/1)	0	0	0
Pta	<i>Potentilla tabernaemontani</i>	<i>Brometalia erecti</i>	0	2 (+/+)	0	4 (+/3)	5 (+/3)	0
Pgr	<i>Prunella grandiflora</i>	<i>Festuco-Brometea</i>	0	0	0	0	0	1 (+/+)
Spr	<i>Salvia pratensis</i>	<i>Festuco-Brometea</i>	1 (+/+)	0	0	0	0	0
Smi	<i>Sanguisorba minor</i>	<i>Festuco-Brometea</i>	2 (+/1)	4 (+/1)	1 (+/+)	5 (1/1)	5 (+/+)	0
Sgr	<i>Scabiosa gramuntia</i>	<i>Festuco-Brometea</i>	2 (+/+)	0	0	0	0	0
Sot	<i>Silene otites</i>	<i>Festuco-Brometea</i>	3 (+/1)	2 (+/+)	0	0	0	0
Sre	<i>Stachys recta</i>	<i>Festuco-Brometea</i>	0	1 (1/1)	2 (+/+)	0	1 (+/+)	0
Spe	<i>Stipa pennata</i>	<i>Festucetalia valesiaca</i>	1 (+/+)	1 (+/+)	0	2 (1/1)	4 (+/3)	0
Tla	<i>Taraxacum laevigatum</i>	<i>Festuco-Brometea</i>	0	0	0	0	4 (+/+)	0
Tch	<i>Teucrium chamaedrys</i>	<i>Festuco-Brometea</i>	1 (+/+)	5 (1/20)	4 (1/6)	2 (1/1)	4 (+/2)	2 (1/2)
Tmo	<i>Teucrium montanum</i>	<i>Festuco-Brometea</i>	0	4 (+/+)	1 (+/+)	0	0	0
Tli	<i>Thesium linophyllum</i>	<i>Festuco-Brometea</i>	0	0	0	0	2 (+/+)	1 (+/+)
Thu	<i>Thymus humifusus</i>	<i>Festuco-Brometea</i>	0	4 (+/+)	0	0	0	3 (+/+)
<i>Juncetea trifidi</i> and subordinated units								
Apy	<i>Ajuga pyramidalis</i>	<i>Caricetalia curvulae</i>	0	1 (+/+)	0	0	0	0
<i>Koelerio-Corynephoretea</i> and subordinated units								
Aar	<i>Acinos arvensis</i>	<i>Koelerio-Corynephoretea</i>	1 (+/+)	1 (+/+)	0	0	0	0
Aay	<i>Alyssum alyssoides</i>	<i>Alysso-Sedion albi</i>	0	0	0	0	2 (+/+)	0
Evu	<i>Echium vulgare</i>	<i>Koelerio-Corynephoretea</i>	2 (+/+)	0	0	1 (+/+)	0	0
Hpe	<i>Hieracium peletierianum</i>	<i>Sedo-Scleranthetalia</i>	4 (+/3)	5 (+/+)	2 (+/1)	5 (1/10)	5 (+/+)	3 (+/+)
Mfs	<i>Minuartia fastigiata</i>	<i>Alysso-Sedion albi</i>	3 (+/1)	0	0	0	0	0
Ppr	<i>Petrorhagia prolifera</i>	<i>Koelerio-Corynephoretea</i>	3 (+/2)	0	0	0	0	0
Psa	<i>Petrorhagia saxifraga</i>	<i>Koelerio-Corynephoretea</i>	1 (+/+)	0	0	1 (+/+)	0	0
Smo	<i>Sedum montanum</i>	<i>Sedo-Scleranthetalia</i>	0	0	0	0	1 (+/+)	0
Ste	<i>Sempervivum tectorum</i>	<i>Sedo-Scleranthetalia</i>	0	0	0	1 (+/+)	1 (+/+)	2 (+/+)
<i>Lygeo-Stipetea</i> and subordinated units								
Lco	<i>Leopoldia comosa</i>	<i>Brachypodietalia phoenicoides</i>	2 (+/+)	0	0	0	0	0
Tcr	<i>Tragopogon crocifolius</i>	<i>Brachypodietalia phoenicoides</i>	0	1 (+/+)	0	0	0	0
<i>Molinio-Arrhenatheretea</i> and subordinated units								
Far	<i>Festuca arundinacea</i>	<i>Potentillo-Polygonetalia</i>	2 (+/+)	0	0	0	0	0
Gcn	<i>Gymnadenia conopsea</i>	<i>Molinietales caeruleae</i>	0	0	0	0	0	1 (+/+)
Lhi	<i>Leontodon hispidus</i>	<i>Arrhenatheretalia elatioris</i>	0	0	0	0	2 (+/+)	0
Lcr	<i>Lotus corniculatus</i>	<i>Molinio-Arrhenatheretea</i>	4 (+/+)	3 (+/+)	5 (1/6)	5 (1/3)	5 (+/+)	1 (1/1)
Ppa	<i>Poa pratensis</i>	<i>Molinio-Arrhenatheretea</i>	2 (+/+)	0	0	0	2 (+/+)	2 (+/+)
Tof	<i>Taraxacum officinale</i>	<i>Arrhenatheretalia elatioris</i>	3 (+/+)	1 (+/+)	1 (+/+)	1 (+/+)	2 (+/+)	0
<i>Nardetea strictae</i> and subordinated units								
Adi	<i>Antennaria dioica</i>	<i>Nardetea strictae</i>	0	0	0	0	0	1 (+/+)
<i>Pyrolo-Pinetea</i> and subordinated units								
Auv	<i>Arctostaphylos uva-ursi</i>	<i>Juniperion nanae</i>	0	4 (+/32)	4 (6/16)	5 (8/45)	3 (6/8)	4 (+/10)
Amo	<i>Astragalus monspessulanus</i>	<i>Ononido-Pinion</i>	1 (2/2)	1 (1/1)	4 (1/6)	4 (2/6)	2 (+/1)	0
Oro	<i>Ononis rotundifolia</i>	<i>Ononido-Pinion</i>	0	4 (+/+)	1 (6/6)	0	0	0
Psy	<i>Pinus sylvestris</i>	<i>Pyrolo-Pinetea/Erice-Pinetea</i>	1 (+/+)	1 (+/+)	4 (1/9)	5 (12/35)	5 (18/70)	5 (37/75)
Soc	<i>Saponaria ocymoides</i>	<i>Pyrolo-Pinetea</i>	1 (+/+)	4 (+/1)	5 (+/6)	4 (+/1)	5 (+/+)	0
Vru	<i>Viola rupestris</i>	<i>Pyrolo-Pinetea</i>	0	3 (+/+)	0	4 (+/1)	0	2 (+/+)
<i>Quercetea pubescentis</i> and subordinated units								
Cab	<i>Colutea arborescens</i>	<i>Quercetalia pubescenti-sessiliflorae</i>	0	0	3 (+/10)	0	0	0

Hfo	<i>Helleborus foetidus</i>	<i>Quercetea pubescentis</i>	0	0	0	0	2 (+/+)	0
Qpu	<i>Quercus pubescens</i>	<i>Quercetea pubescentis</i>	3 (1/15)	2 (+/1)	3 (5/6)	5 (+/6)	5 (+/30)	0
Sar	<i>Sorbus aria</i>	<i>Quercetea pubescentis</i>	0	0	0	0	0	3 (+/1)
<i>Quercetea robori-sessiliflorae</i> and subordinated units								
Bpe	<i>Betula pendula</i>	<i>Quercetea robori-sessiliflorae</i>	0	1 (+/+)	2 (2/5)	0	0	1 (3/3)
Lmo	<i>Lathyrus montanus</i>	<i>Quercetea robori-sessiliflorae</i>	0	0	0	0	0	2 (+/1)
Ptr	<i>Populus tremula</i>	<i>Quercetea robori-sessiliflorae</i>	1 (2/2)	1 (1/1)	5 (5/28)	4 (+/5)	4 (+/26)	3 (+/20)
Vof	<i>Veronica officinalis</i>	<i>Quercetea robori-sessiliflorae</i>	0	0	2 (+/1)	0	0	3 (+/+)
Vri	<i>Viola riviniana</i>	<i>Quercetea robori-sessiliflorae</i>	0	0	0	0	2 (+/+)	1 (+/+)
<i>Robinieta</i> and subordinated units								
Aal	<i>Ailanthus altissima</i>	<i>Robinieta</i>	1 (+/+)	0	0	0	0	0
<i>Rosmarineta</i> and subordinated units								
Tvu	<i>Thymus vulgaris</i>	<i>Rosmarineta</i>	1 (+/+)	0	0	0	4 (+/8)	0
<i>Stellarietea mediae</i> and subordinated units								
Ach	<i>Ajuga chamaepitys</i>	<i>Caucalidion lappulae</i>	1 (+/+)	0	0	0	0	0
Cmi	<i>Chaenorhinum minus</i>	<i>Stellarietea mediae</i>	1 (+/+)	0	0	0	0	0
Cal	<i>Chenopodium album</i>	<i>Stellarietea mediae</i>	3 (+/1)	0	0	0	0	0
Car	<i>Cirsium arvense</i>	<i>Stellarietea mediae</i>	2 (5/8)	3 (+/6)	2 (+/+)	1 (+/+)	0	0
Cca	<i>Conyza canadensis</i>	<i>Stellarietea mediae</i>	5 (1/8)	0	0	0	0	0
Dte	<i>Diplotaxis tenuifolia</i>	<i>Sysimbretalia</i>	1 (1/1)	1 (1/1)	0	0	0	0
Ola	<i>Odontites lanceolata</i>	<i>Caucalidion lappulae</i>	2 (1/10)	0	0	0	0	0
Vsa	<i>Vicia sativa</i>	<i>Stellarietea mediae</i>	1 (+/+)	0	0	0	0	0
Var	<i>Viola arvensis</i>	<i>Stellarietea mediae</i>	2 (+/+)	0	0	0	0	0
<i>Thero-Brachypodietea</i> and subordinated units								
Cvl	<i>Crupina vulgaris</i>	<i>Thero-Brachypodietea</i>	2 (1/1)	0	0	0	0	0
Lsm	<i>Linaria simplex</i>	<i>Thero-Brachypodietea</i>	1 (+/+)	0	0	1 (+/+)	0	0
Mmi	<i>Medicago minima</i>	<i>Thero-Brachypodietea</i>	1 (+/+)	0	0	0	0	0
<i>Thlaspietea rotundifolii</i> and subordinated units								
Aca	<i>Achnatherum calamagrostis</i>	<i>Stipetalia calamagrostis</i>	0	4 (+/6)	0	1 (1/1)	0	0
Ena	<i>Erucastrum nasturtiifolium</i>	<i>Epilobion fleischeri</i>	0	2 (+/+)	1 (1/1)	0	0	0
Hpi	<i>Hieracium piloselloides</i>	<i>Epilobion fleischeri</i>	0	2 (1/1)	0	1 (+/+)	0	0
<i>Trifolio-Geranietea sanguinei</i> and subordinated units								
Ctr	<i>Centaurea triumfetti</i>	<i>Geranion sanguinei</i>	0	0	1 (+/+)	0	0	1 (+/+)
Cvr	<i>Coronilla varia</i>	<i>Origanetalia vulgaris</i>	0	2 (+/+)	4 (+/6)	0	0	2 (+/+)
Hpr	<i>Hypericum perforatum</i>	<i>Origanetalia vulgaris</i>	1 (1/1)	0	2 (1/6)	0	0	0
Ico	<i>Inula conyza</i>	<i>Origanetalia vulgaris</i>	1 (+/+)	0	0	1 (+/+)	0	0
Lsi	<i>Laserpitium siler</i>	<i>Geranion sanguinei</i>	0	2 (1/6)	1 (+/+)	0	0	2 (+/1)
Mfa	<i>Medicago sativa</i> ssp. <i>falcata</i>	<i>Geranion sanguinei</i>	0	0	0	0	3 (+/1)	0
Por	<i>Peucedanum oreoselinum</i>	<i>Geranion sanguinei</i>	0	1 (+/+)	1 (+/+)	0	0	0
Sit	<i>Silene italica</i>	<i>Geranion sanguinei</i>	0	1 (+/+)	3 (+/1)	1 (+/+)	3 (+/+)	0
Snu	<i>Silene nutans</i>	<i>Trifolio-Geranietea sanguinei</i>	0	0	0	0	0	1 (+/+)
Tme	<i>Trifolium medium</i>	<i>Trifolium medii</i>	0	0	1 (1/1)	0	0	1 (+/+)
Vly	<i>Verbascum lychnitis</i>	<i>Origanetalia vulgaris</i>	3 (+/3)	0	0	0	0	0
<i>Vaccinio-Piceetea excelsae</i> and subordinated units								
Cap	<i>Clematis alpina</i>	<i>Piceenion excelsae</i>	0	0	0	0	2 (+/2)	0
Lde	<i>Larix decidua</i>	<i>Piceenion excelsae</i>	0	0	1 (1/1)	1 (1/1)	3 (1/17)	0
Msy	<i>Melampyrum sylvaticum</i>	<i>Vaccinio-Piceetea excelsae</i>	0	0	0	0	0	5 (1/10)

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Pex	<i>Picea excelsa</i>	<i>Vaccinio-Piceetea excelsae</i>	0	0	0	1 (+/+)	1 (+/+)	2 (+/3)
Pun	<i>Pinus uncinata</i>	<i>Piceetalia excelsae</i>	0	0	0	0	1 (1/1)	0
Vmy	<i>Vaccinium myrtillus</i>	<i>Vaccinio-Piceetea excelsae</i>	0	0	0	0	0	1 (+/+)

References

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